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Growth and demography of paua *Haliotis iris* (Mollusca: Gastropoda) in northeastern New Zealand

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Abstract

The growth and demography of an unfished population of paua (*Haliotis iris*) was examined within a marine reserve on the northeastern coast of New Zealand from 1986 to 1991. Size-frequency analysis showed that recruitment of paua was regular and annual. Paua were found and measured in the field down to 4 mm shell length and juvenile paua were individually tagged down to 8 mm shell length. Growth estimates from tag-recapture and size-frequency analysis revealed that paua grew rapidly to a size of at least 70 mm shell length in approximately 3 years. Growth then slowed abruptly with negligible growth beyond 80 mm. In contrast to studies in other areas, paua rarely reached the legal takeable size of 125 mm. Tag-recapture studies revealed large variability in growth of the juvenile paua. The differences in growth and demography between southern and northern populations of paua has important implications for the future management of northern paua populations.

Introduction

Abalone (*Haliotis* spp.) form important commercial fisheries in temperate coastal waters around the world (Mottet, 1978). Good management of these fisheries requires a sound understanding of the biology and demography of the species.

In New Zealand, there are three species of abalone which are known under the collective name of paua (see Poore, 1969 for a review of the biology of these species). *Haliotis iris* Gmelin 1791, (the common or black-foot paua) is the largest, most abundant, and most commercially sought after. Most research on *Haliotis iris* has been concentrated in southern localities of New Zealand (Poore, 1969; 1972a; b; c; 1973; Sainsbury, 1982a; b; McShane *et al.*, 1988; Schiel and Breen, 1991; McShane *et al.*, 1994a; McShane *et al.*, 1994b; McShane and Naylor, 1995a; McShane and Naylor, 1995b). Although the northern New Zealand commercial paua fishery accounts for a small proportion of the total annual catch, recreational and traditional harvesting of paua in northern New Zealand is still extremely important. Apart from a preliminary survey by Dickson (1987) and a description of the reproductive biology of a northern population (Hooker and Creese, 1995), there have been no published studies from populations north of Coromandel. Although the McShane *et al.* (1994a) study on 61 populations of *H. iris* covers a wide geographic range, it does not include sites north of the Coromandel Peninsula. Many previous studies on gastropods have shown large spatial variability in population size structures, growth rates, recruitment and survival patterns (Underwood, 1979; Day and Fleming, 1992; McShane *et al.*, 1995a; McShane *et al.*, 1995b). It is therefore likely that demographic information from southern populations of *Haliotis iris* in New Zealand may not apply to northern populations. Densities of *Haliotis iris* in the most suitable habitats within the Leigh Marine Reserve (which has been totally protected since 1976 and might therefore be expected to

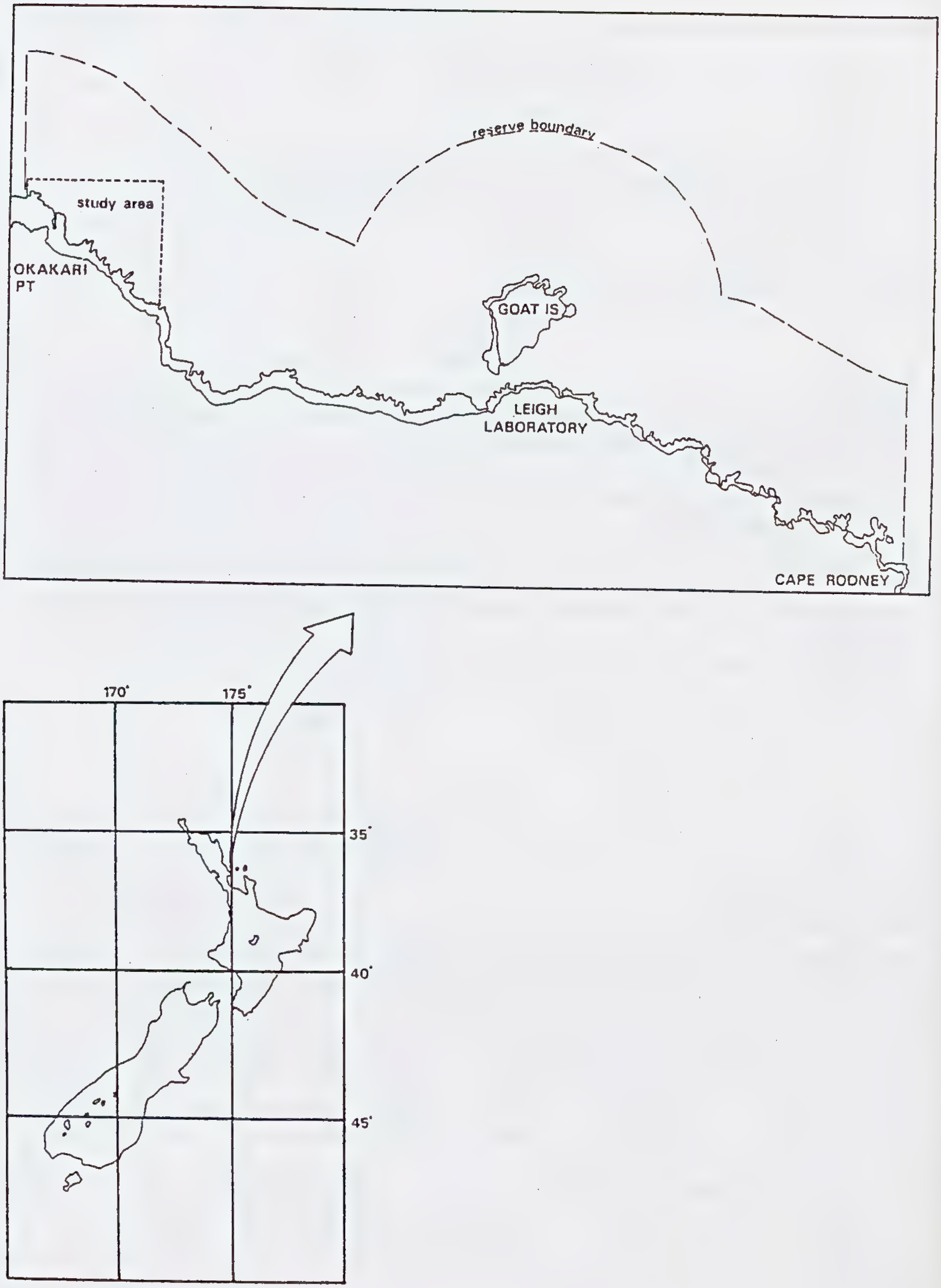

Figure 1 Map of the North Island of New Zealand showing the location of the study area at Okakari Point in the Leigh Marine Reserve and the nearby University of Auckland's Marine Laboratory.

have near natural population sizes) range from 6 to 14 m^{-2} (Hooker and Jeffs, unpubl. data). This compares with densities of 16 to 60 m^{-2} reported by Sainsbury (1982a) for southern populations. *Haliotis iris* in the Leigh Marine Reserve rarely reach 110 mm in length, lower than the minimum legal size of 125 mm and well below sizes of 160–170 mm commonly reached by paua from the South Island (Poore, 1969; Sainsbury, 1982a).

This paper describes a study of an unfished population of *H. iris* over six years (1986–1991) in northeastern New Zealand. The aim of this study was to examine and quantify habitat utilisation, temporal changes in population size structure and growth, and to link previously published information on the reproductive cycle of northern paua (Hooker and Creese, 1995) with the observed recruitment of juveniles into the population. Finally, we make larger spatial scale comparisons of our work to previous work on *H. iris* populations from southern localities.

Methods

The research was carried out in the Cape Rodney to Okakari Point Marine Reserve near Leigh (36°16'S, 174°48'E), hereafter referred to as the Leigh Marine Reserve (Fig. 1). The physical and biological characteristics of subtidal habitats in this area are described by Ayling (1976), Leum and Choat (1980), and Creese (1988).

Microhabitat and depth distribution: In November 1987, three sites (approximately 100 m apart) were selected at Okakari Point at the northern end of the Leigh Marine Reserve (Fig. 1). At each of the three sites a 60 m tape was laid out perpendicular to the shore, starting from the upper limit of the sublittoral fringe (*sensu* Morton and Miller, 1973). The transects were of sufficient length to extend from the sublittoral fringe through the "shallow broken rock" and into areas of "bare rock" habitat (*sensu* Ayling 1978). Paua are rarely found in any of the deeper habitat types (>10 m) within the reserve. A single quadrat (1 m^2) was sampled every second metre along the length of the transect while SCUBA diving. All paua in each quadrat were counted and measured *in situ* to the nearest millimetre using vernier callipers. The position of each paua was also designated to one of three microhabitats:

1. Cryptic: totally hidden under boulders so the paua could not be seen until the boulder was moved.
2. Partially Exposed: the paua could be seen without moving the boulder, but was partially hidden.
3. Exposed: the paua was totally out in the open and easily seen without moving any boulders.

Each transect was arbitrary divided into three twenty metre sections, which roughly corresponded to different depth strata. The first section (shallow) corresponded to 0–2 m depth below the sublittoral fringe. The second section (mid) corresponded to 2–4 m depth from the sublittoral fringe and the third section (deep) corresponded to 4–6 m. The substratum is extremely variable over this depth range, consisting of large flat sections of bed-rock with small caves and crevices, or large boulders and vertical bed-rock (2–5 m high) intermingled with smaller boulders and pebbles.

Morphometric relationships in paua: To test the assumption that shell length is an adequate measurement of animal size, a size range of adult paua were collected monthly (as described in Hooker and Creese, 1995) along with collections of smaller individuals. The shells of all animals were measured, and then each animal was removed from its shell, drained of excess water and weighed.

To assess whether wet weight measurements were an adequate description of weight, a sample of paua was dried in an oven at 78°C. After one week the animals were removed and re-weighed to the nearest 0.1 gram, and correlations obtained for the relationship between wet and dry weights.

Tagging: Adult paua were tagged using numbered plastic tags which were attached with stainless steel wire threaded though the most posterior respiratory pore. Paua could be reliably tagged down to a size of approximately 70 mm by this method, but in smaller paua the wire pulled through the thinner shell. A small number (29) of adult paua were tagged by using a small amount of a two-part epoxy putty, which was pressed onto the shell near the apex, and a plastic tag was then embedded into the putty. Approximately 1300 adult paua were tagged between October 1986 and February 1987 at four sites within the Leigh Marine Reserve, two at Okakari Point, one at Te Rere Bay and one at Cape Rodney at the southern end of the Marine Reserve (Fig. 1). All paua to be tagged were carefully removed from the rock surface, taken to a nearby intertidal rock platform, tagged and measured, then replaced as soon as possible. Tagged adults were re-measured twice in 1987 (June and October), and a small number (16) were re-measured at one site in early 1990. The tagged animals were re-measured *in situ* where possible.

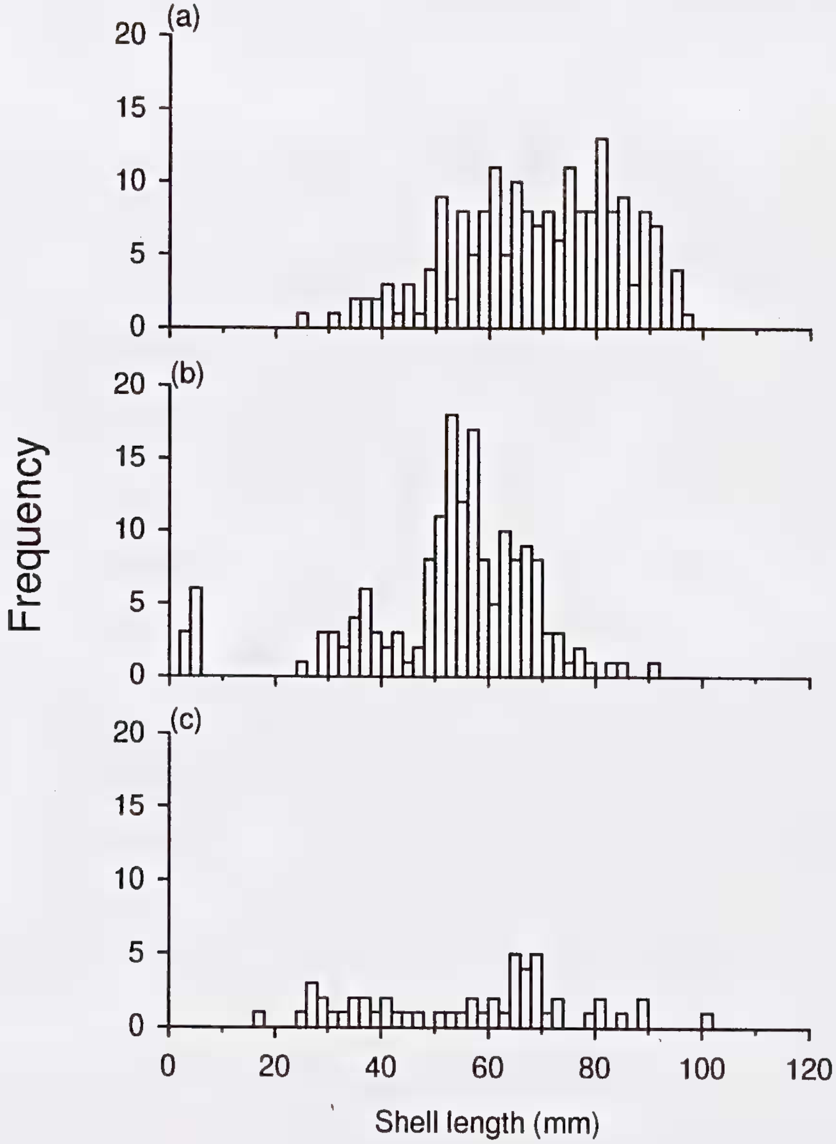

Figure 2 Length frequency distributions of the three transects combined and stratified with respect to distance from the shore. (a), shallow (0–20 m from sublittoral fringe) n=187. (b), mid depth (20–40 m from sublittoral fringe) n=166. (c), deep 40–60 m from sublittoral fringe) n=52.

Approximately 800 juveniles were tagged in the field at four sites at Okakari Point in February 1987. Tagged juveniles were returned to their original sites within a few minutes to minimise possible tagging effects. All juvenile paua (<70 mm) were tagged using numbered plastic tags (Hallprint), fixed to the clean exterior shell of the paua with cyanoacrylate-glue. A further sample of juveniles was tagged in May 1987, when the juvenile paua from the first tagging were also remeasured. All tagged juveniles were remeasured in October 1987. This was accomplished by methodically searching all boulders in the tagging site and the surrounding area.

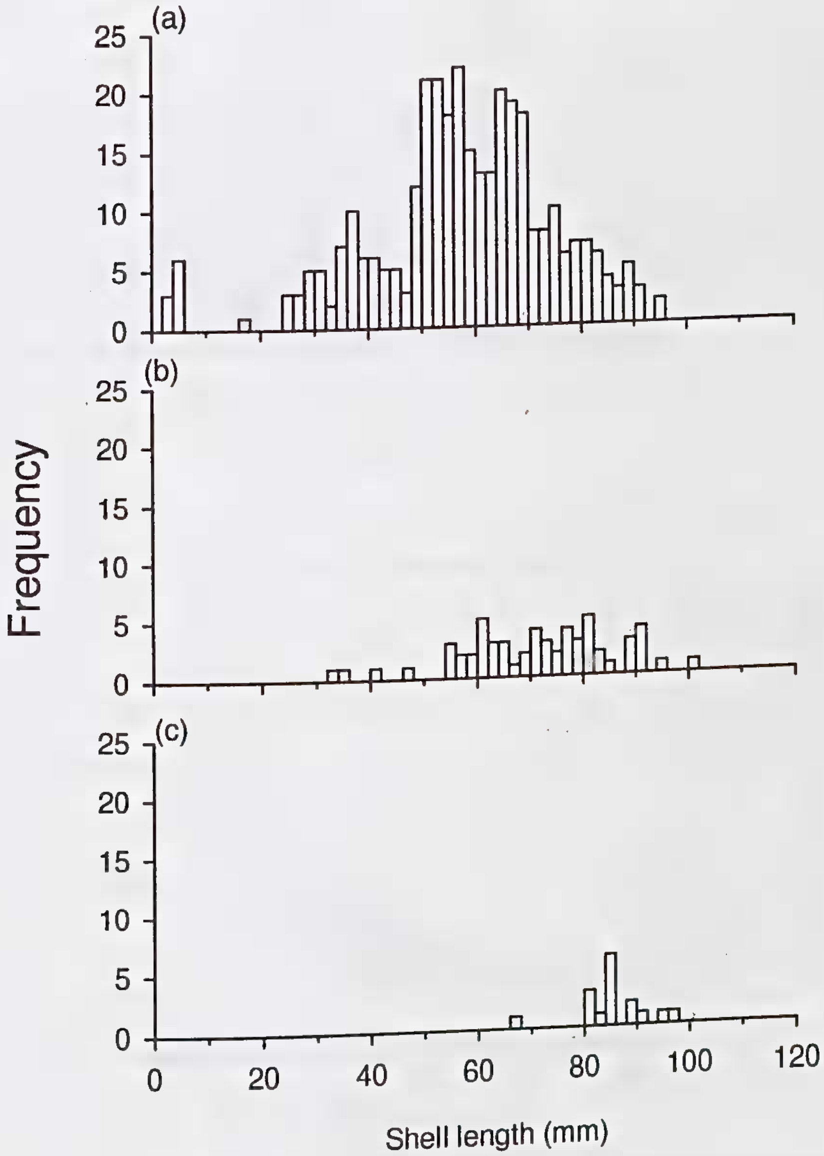

Figure 3 Length frequency distributions of the three transects combined and divided with respect to micro-habitat use. (a), "Cryptic" paua were totally hidden under boulders, n=331. (b), "semi-exposed" paua could be seen without moving the boulder but were partially hidden, n=58. (c) "exposed" paua were totally out in the open, n=16.

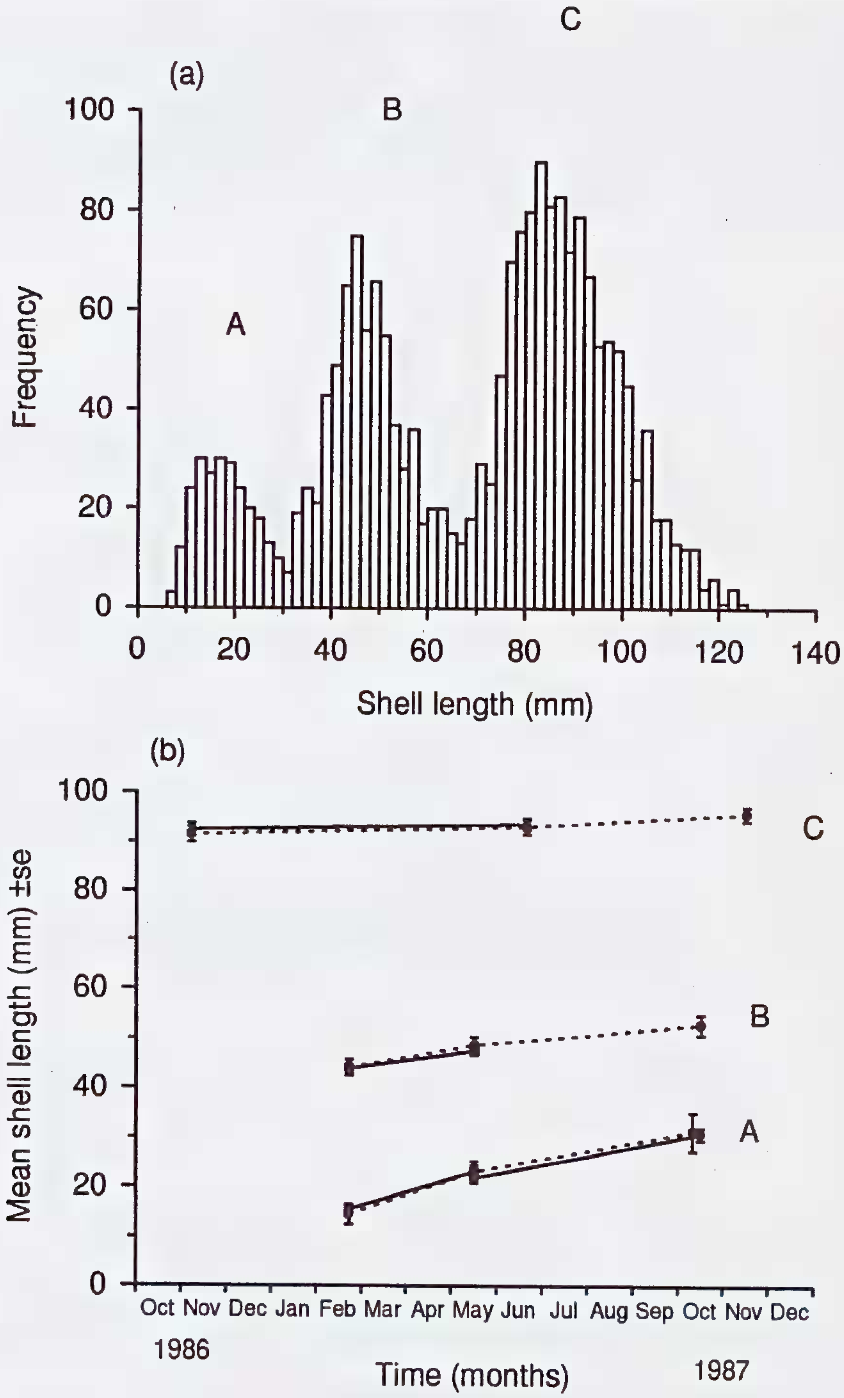

Figure 4 (a) Length frequency distribution of the initial lengths of all tagged paua from the Leigh Marine Reserve. (b) Growth of the mean size of each of the three tagged cohorts from (a). The dashed line represents paua that were recaptured twice.

Population sampling: Paua were measured in the boulder habitat at Okakari Point on 12 occasions between February 1986 and February 1991. A 1 m^2 square quadrat was thrown haphazardly into areas of boulders. Each quadrat was methodically searched by turning over all moveable boulders. All paua found were measured and replaced onto the boulders. This procedure was repeated until at least 200 paua had been measured. Cohorts were identified and their mean lengths and standard deviations calculated using polymodal size-frequency analysis (ELEFAN; Pauly and David, 1980; Pauly and Ingles, 1981).

Results

Microhabitat and depth distribution: There were only slight differences in population structure on the three transects. New recruits were found only on the third transect. Mean densities (± standard error) were 6.1 ± 2.2. m^{-2} for transect one, 2.6 ± 0.8. m^{-2} for transect two and 4.5 ± 1.8. m^{-2} for transect three. Paua were less abundant further from shore (Fig. 2), in slightly deeper water, where there was less boulder habitat with more areas of flat bed-rock and sand. Although the full size range of paua was found at all depths, there was a tendency for more larger animals in shallow water. When the transects were pooled across the three micro-habitats (Fig. 3), paua of all sizes were mostly cryptic (81.7%). Very few paua (only 4%) were found totally out in the open, and all but one of these exposed individuals were over 80 mm in length.

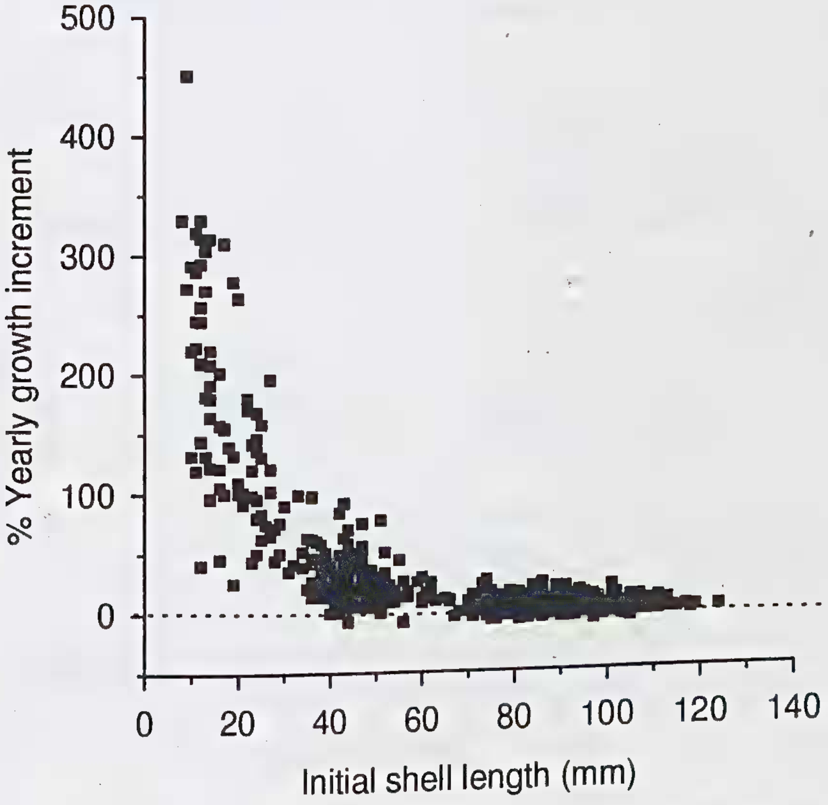

Figure 5 Plot of the percentage growth increment, standardised to one year's growth, versus the initial length of all tagged paua. Growth increments below zero are measurement errors that have been multiplied to a year's growth.

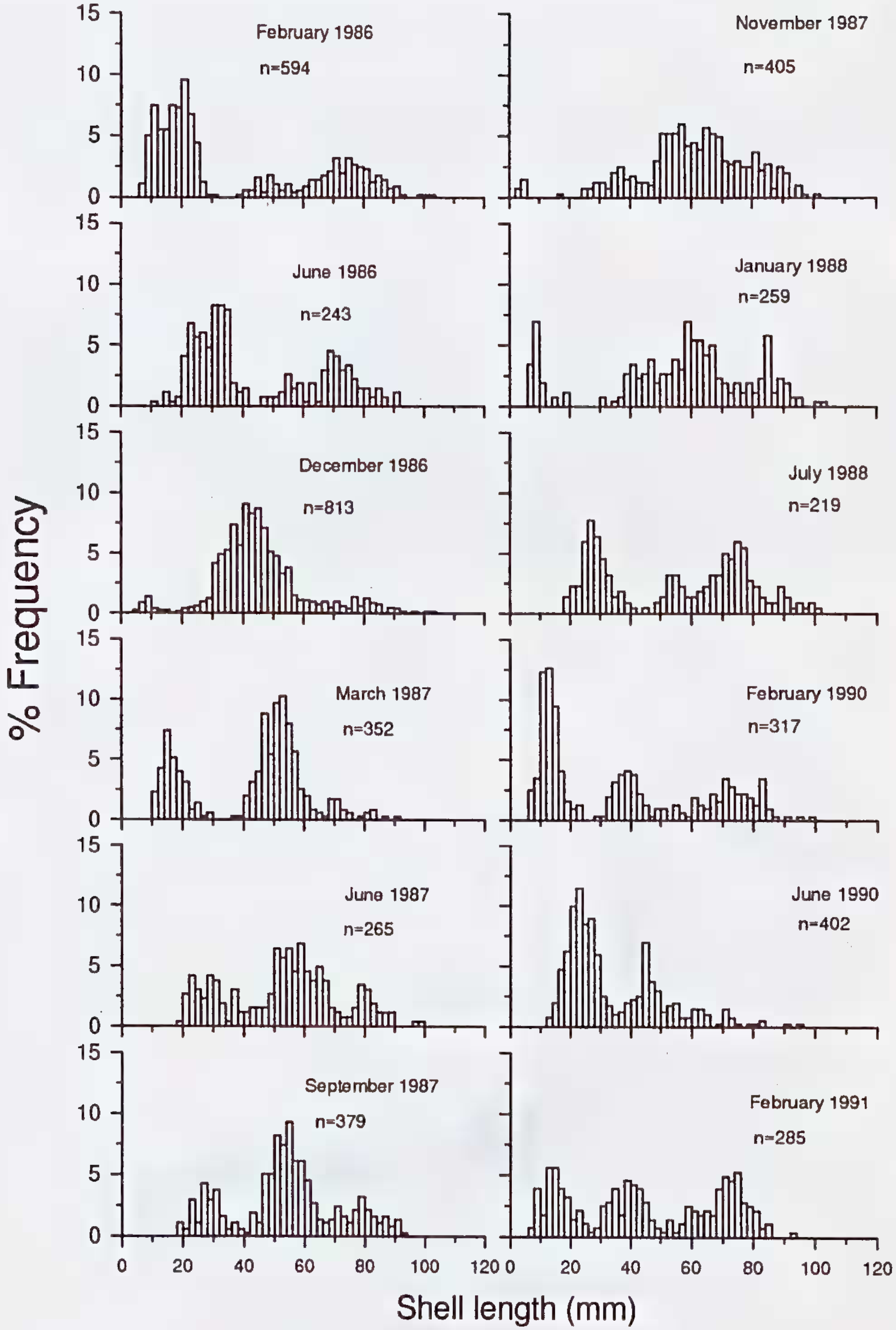

Figure 6 Length frequency histograms of juvenile paua at Okakari Point from February 1986 to February 1991. Samples were collected from within the boulder habitat where there are mainly juvenile paua and therefore underestimate the adult fraction in the population.

Morphometric relationships: The correlation between wet weight and dry weight of paua over the whole range of sizes had an r^2 value of 0.998, indicating that wet weight was an adequate estimator of weight. The shell length to body weight relationship throughout the size range was calculated as $W=0.0000236\ L^{3.29}$ (W=wet body weight in g; L = shell length in mm).

Tag-recapture: The initial lengths of tagged paua fell into three distinct cohorts (Fig. 4a) which were representative of the paua population at Okakari Point at that time. The recapture of tagged paua was not biased to any particular size group with a similar proportion of each of the three cohorts being subsequently recovered. An estimate of the growth rate of the three groups of tagged paua was obtained by plotting the mean length of each cohort against time (Fig. 4b). Assuming that spawning occurred around August/September (Hooker and Creese, 1995; see also Fig. 7), it is clear that the first mode in Fig. 4a consists of 0+ animals and hence that newly settled paua grew to approximately 30 mm in their first year and to approximately 52 mm in their second year. The slope of the line changes between sampling periods (Fig. 4b) suggesting seasonal variations in growth with a smaller mean increase in length over the winter months.

Growth of smaller tagged paua was highly variable (Fig. 5). For individuals less than 25 mm, the annual increase in length varied from 450% to under 50%. Increments in shell length were smaller and much less variable for paua larger than 25 mm. The annual growth increment approached zero at around 75 mm in length and growth beyond this size was very slow.

Population sampling: The twelve samples collected from Okakari Point from February 1986 to February 1991 show discrete modal size-classes, suggesting strong pulses of recruitment between August and October each year (Fig. 6). Juveniles grew rapidly from the size at which they were first detected to merge with the adult mode after approximately three years. The mean size of the largest cohort stayed relatively constant through time. Because sampling was restricted to the boulder habitat, only the smaller cohorts were adequately represented; paua over 80 mm were mostly found outside this habitat. The ELEFAN software package fits normal curves to polymodal frequency distributions. In all but one case (the first sample in February 1986) the fitted curves did not differ significantly from the actual data sets (c^2 goodness-of-fit tests, $P<0.05$, d.f. ranging from 13 to 24). The mean sizes of the cohorts of juvenile paua, as determined by the ELEFAN analysis, are plotted on a linear time scale in Fig. 7. Estimates of growth of larger animals were not possible as the older cohorts coalesced above approximately 70 mm.

From 1986 to 1991 paua grew from 31 to 35 mm in their first year, and reached 55 to 60 mm in their second year (Fig. 7). Separation of the 2+ cohort was not always possible as cohorts had either coalesced or the information could not be reliably derived from the data. However, the general trend was for the cohorts to reach at least 70 mm by the end of their third year in the boulder field (Fig. 7). A possible seasonal component to the growth of paua in this sub-population was apparent over the winter (June to September) of 1987 when growth of all cohorts slowed markedly (Fig. 7).

Similar estimates of growth were obtained from the analyses of the size-frequency data and the tag-recapture data during the period February to October 1987. The mean size of tagged paua in February 1987 was 14 mm (Fig. 4b) and the estimated size of the corresponding cohort in the population size-frequency analysis was the same (Fig. 7). The tagging data revealed that the cohort had grown to a mean size of 23 mm by May 1987 and estimates from the size frequency analysis for this month also estimated the cohort at approximately 23 mm. By October 1987 the tagging data showed that the mean size of the cohort was 31 mm (Fig. 4b) and the size frequency analysis again gave the same result (Fig 7). This strongly suggests that tagging had a negligible effect on the growth rate of paua and that polymodal size frequency analysis was an accurate technique for assessing growth in this sub-population.

Discussion

Several haliotid species are known to show depth-related patterns (Poore, 1972c; Shepherd, 1973;

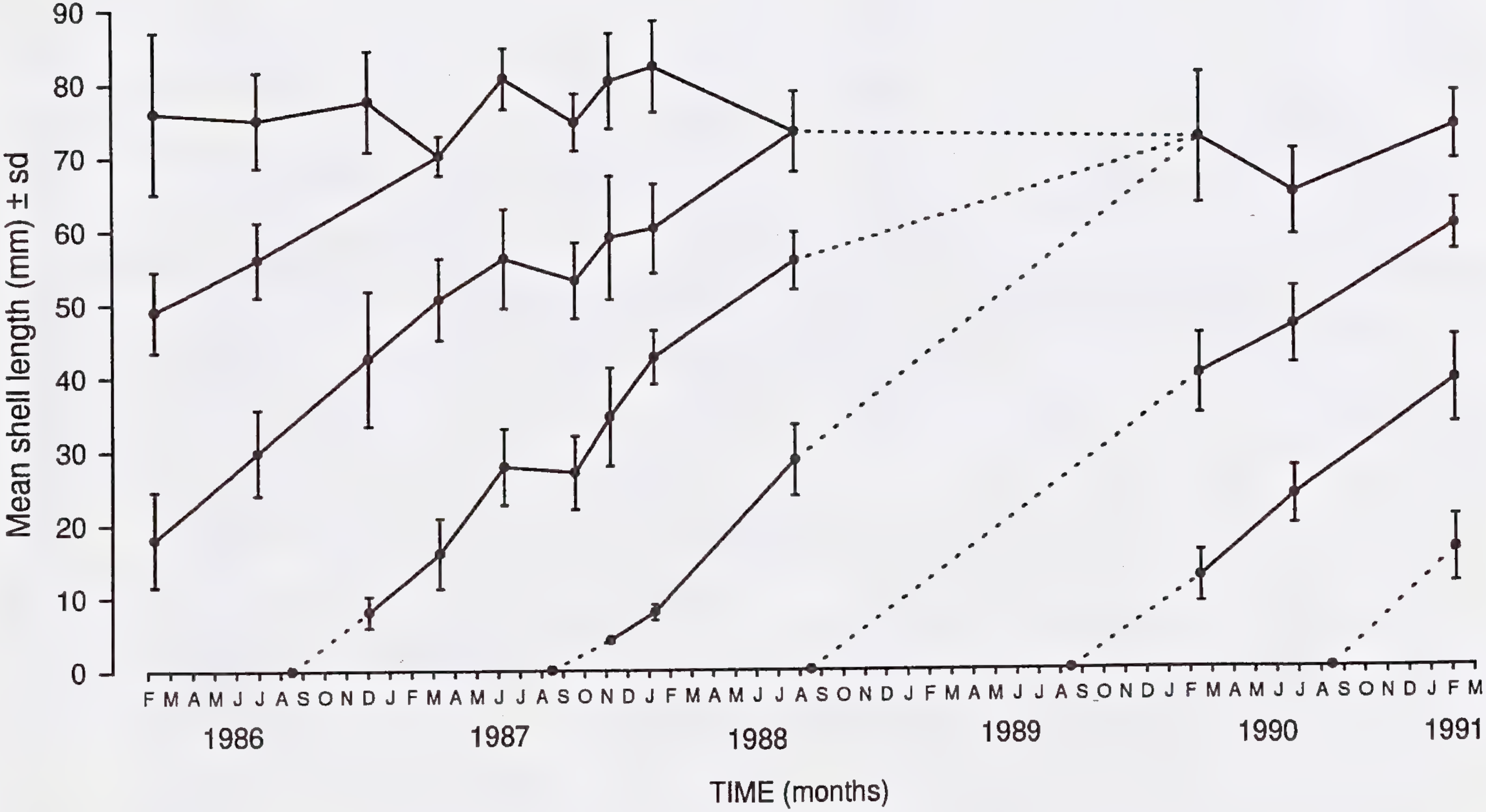

Figure 7 Mean length of cohorts, on a linear time scale, derived from length frequency histograms from February 1986 to February 1991 (Fig. 7). Error bars are standard deviation. Dashed lines represent areas of uncertain growth of cohorts and lines extrapolated back to the probable time of settlement (spawning) estimated from reproductive studies (Hooker and Creese, 1995).

Witherspoon, 1975; Schiel, 1992). In this study there was not a consistent change in population structure with depth for *H. iris* in the Leigh Marine Reserve. Any difference in population structure is possibly an artefact of available habitat rather than determined by depth itself. Both juvenile and adult paua can be found across the depth range sampled if there is suitable habitat (Hooker and Jeffs, unpubl. data).

Spatial separation of age cohorts on the basis of microhabitat type has been shown to be important for abalone in southern Australia (Shepherd, 1973; Prince *et al.*, 1988; Witherspoon, 1975; Shepherd and Turner, 1985), and for *H. iris* in southern New Zealand where paua begin to emerge from their cryptic habitat at the onset of sexual maturity (Schiel, 1992; McShane and Naylor, 1995a). Paua within the Leigh Marine Reserve do not appear to emerge from the cryptic habitat at the onset of sexual maturity (50–60 mm SL, Hooker and Creese, 1995). Although, there was a tendency for larger paua to be more exposed than smaller animals, paua of all sizes were still found under boulders and very few paua were seen on exposed surfaces at these sites. This is different from the pattern found for other haliotid species and for *H. iris* in southern localities. This difference of depth distribution and micro-habitat utilisation between *H. iris* in the Leigh Marine Reserve and more southern localities in New Zealand may simply be due to the much greater densities of paua found in southern populations, thus limiting the cryptic habitat available to the larger paua.

The size-frequency distributions from Okakari Point show single annual recruitment pulses in the years 1985–1990. However, reproductive studies of paua at Leigh showed that multiple spawnings occur over the late winter to early spring period (July to September) (Hooker and Creese, 1995; Neill, 1997), suggesting that successful recruitment may result from only one particular spawning event or alternatively that multiple settlements coalesced very rapidly into a single year class (Day and Fleming, 1992). Recruitment was observed in December 1986, with the emergence of a 0+ cohort with a mean size of approximately 8 mm SL and in November 1987 with a mean size of approximately 4 mm SL. Spawning and settlement in *Haliotis iris* are separated by less than 14 days (Tong *et al.,* 1987; Moss and Tong, 1992), and newly settled juveniles grow to 3–4 mm SL in 1–2 months. The observed recruitment in November/December therefore most likely originated from the late winter to early spring spawning, *i.e.* when the seawater starts to warm up from the annual minimum in August/September.

Growth of haliotids is often summarised by fitting growth curves of the von Bertalanffy type (Forster, 1967; Newman, 1968; Poore, 1972c; Hayashi, 1980; Sainsbury, 1982a; Shepherd and Hearn, 1983; Keesing and Wells, 1989; Day and Fleming, 1992). While useful in predicting future growth trends (in fished populations for example) and assuming that the assumptions of these growth models have been met (something that is not always explicitly demonstrated), it is often difficult to assess whether the generated growth curves adequately describe the actual growth of the population because few raw data are presented in scientific publications. It may be possible, for instance, to over- or under-estimate early growth (Poore, 1972c) or to obtain a wide range of growth estimates from a given set of size data (Grant *et al.*, 1987; Prince *et al.*, 1988). Although our size-frequency data covered a reasonable time span (5 years), they came from a restricted habitat that did not include the full size range of paua, and there was also an 18 month gap in the time series. The tagging data covered a full size range of animals, but was restricted to a period of less than one year. Although the combination of these two data sets allowed us to confidently describe the growth patterns of paua in the Leigh Marine Reserve, we can see no merit in using them at this time to derive additional growth parameters for use in von Bertalanffy models.

Analysis of the tag-recapture and size-frequency analysis on raw data demonstrates that paua in the Leigh Marine Reserve grow to approximately 28–35 mm in their first year, 50–55 mm in their second year and 70–75 mm in their third year. Growth beyond 80 mm SL was negligible. This result is different from that obtained by Poore (1972c) and Sainsbury (1982a) for southern populations. Comparison of the growth rate of paua in the Leigh Marine Reserve population with that obtained by Poore (1972c) and Sainsbury (1982a) shows that paua at Leigh have an initially faster growth rate than southern paua to approximately three years old, but that growth slows abruptly after approximately 80 mm. Southern paua have a slower initial growth rate but keep growing to a much larger maximum size than paua in this northern locality.

Paua in the Leigh Marine Reserve seldom reached sizes greater than 100–110 mm, with most adults averaging 70–90 mm. The largest tagged paua was 124 mm, and only two paua, of 126 mm each, were found over the legal size limit on the coast adjacent to the Leigh Marine Reserve. In southern paua populations, it is not uncommon for paua over 160 mm to be found, and Poore (1969) recorded an individual of 177 mm SL. The mean shell length from samples of adult *H. iris* from 61 populations from around New Zealand revealed that three out of the four populations in the northern half of the North Island were below 100 mm and all southern populations had a mean shell length over 100 mm (McShane *et al.,* 1994a)

Subtle small scale (hundreds of metres) ecological differences in abalone populations have been found to be important for their management (McShane and Naylor, 1995a). Marked differences in the ecology of *Haliotis iris* populations have been demonstrated here on a larger geographic scale (hundreds of kilometres). Northern paua populations have important demographic differences compared to southern populations. Their reproductive cycle is substantially different (Hooker and Creese, 1995), their habitat utilisation, densities and growth characteristics (as described here) are all different from southern populations. These differences will have important implications for the management and possibly aquaculture of this species in northern New Zealand.

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